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Leguminosae plants play a key role in affecting soil physical-chemical and biological properties during grassland succession after farmland abandonment in the Loess Plateau, China

SUN Lin, YU Zhouchang, TIAN Xingfang, ZHANG Ying, SHI Jiayi, FU Rong, LIANG Yujie, ZHANG Wei*

College of Grassland Agriculture, Northwest A&F University, Yangling 712100, China

Abstract: Leguminosae are an important part of terrestrial ecosystems and play a key role in promoting soil nutrient cycling and improving soil properties. However, plant composition and species diversity change rapidly during the process of succession, the effect of leguminosae on soil physical-chemical and biological properties is still unclear. This study investigated the changes in the composition of plant community, vegetation characteristics, soil physical-chemical properties, and soil biological properties on five former farmlands in China, which had been abandoned for 0, 5, 10, 18, and 30 a. Results showed that, with successional time, plant community developed from annual plants to perennial plants, the importance of Leguminosae and Asteraceae significantly increased and decreased, respectively, and the importance of grass increased and then decreased, having a maximum value after 5 a of abandonment. Plant diversity indices increased with successional time, and vegetation coverage and above- and below-ground biomass increased significantly with successional time after 5 a of abandonment. Compared with farmland, 30 a of abandonment significantly increased soil nutrient content, but total and available phosphorus decreased with successional time. Changes in plant community composition and vegetation characteristics not only change soil properties and improve soil physical-chemical properties, but also regulate soil biological activity, thus affecting soil nutrient cycling. Among these, Leguminosae have the greatest influence on soil properties, and their importance values and community composition are significantly correlated with soil properties. Therefore, this research provides more scientific guidance for selecting plant species to stabilize soil ecosystem of farmland to grassland in the Loess Plateau, China.

Keywords: secondary succession; leguminosae; plant diversity; plant community composition; soil physical-chemical properties; soil biological properties

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1 Introduction

Secondary succession is a key measure to restore degraded ecosystems and plays an important role in increasing soil nutrient content and plant diversity (Zeng et al., 2017). During secondary

*Corresponding author: ZHANG Wei (E-mail: zwgwyd@163.com)
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succession, plant productivity and community composition are affected directly (Li et al., 2019; Liu et al., 2019). Some studies have shown that plant characteristics (such as plant biomass, coverage, evenness, and diversity) increased after secondary succession (Fan et al., 2015; Tessema and Belay, 2017), and soil properties may increase with succession due to the increase in plant biomass (Wang et al., 2009; Zhao et al., 2019). Some researchers have shown that natural regeneration through secondary succession can restore degraded soil properties and maintain soil fertility (Li et al., 2019, 2022; Zou et al., 2022; Li et al., 2023). Soil physical-chemical properties are affected by decomposition of plant root exudates and litter decomposition matter due to vegetation growth (Zhao et al., 2015). In addition to soil microbial biomass, ecological enzyme activity is sensitive to changes in soil and plants. Therefore, secondary succession affects soil physical-chemical properties, enzyme activity, and microbial biomass (Zhu et al., 2012).

It has been shown that long-term vegetation succession is a key driver of succession in restored areas (van der Heijden et al., 2008; Lucas-Borja et al., 2019; Hao and Chu, 2021), and that vegetation changes inevitably affect soil nutrient (Reich, 2005; Peichl et al., 2012). Moreover, fast-growing vegetation can affect soil nutrient storage through litter decomposition and root exudates (Berg, 2014; Lozano et al., 2014). van der Putten et al. (2013) found that plants could influence soil microbial communities and drive changes in soil physical-chemical properties. In addition, plants can improve microclimate conditions and increase soil microbial activity, thus promoting soil nutrient cycling and accumulation (Wickander et al., 2021; Bao et al., 2022). In contrast, soil extracellular enzymes are rate-limiting steps of microbial metabolism, affecting microbial decomposition of carbon and nutrients, and their activity is also positively correlated with organic carbon content, affecting soil chemical properties (Chabrerie et al., 2003), but the pattern of change in enzyme activity during long-term natural processes of secondary succession is unclear. And different plant species have different effects on soil because each plant has its own unique biological characteristics that may affect nutrient return and decomposition of organic carbon differently (Fanin and Bertrand, 2016). For example, Leguminosae typically contain high levels of nitrogen, while C_4 plants contain high levels of carbon and can significantly increase nitrogen and carbon contents of soil (Sivaram et al., 2018; Yao et al., 2021). Some studies have shown that rapid decomposition of litter of nitrogen-rich plants can increase soil nutrient content (Horodecki and Jagodzinski, 2017). In addition to interspecific differences, it has also been found that effects of the same plant functional group on soil properties vary depending on successional time (Hu et al., 2016). Thus, the effects of changes in vegetation on soil properties are variable and uncertain during secondary succession (Zhang et al., 2016; Zhang et al., 2022).

There are fewer studies on the effects of Leguminosae on soil properties (Fterich et al., 2014), and the potential mechanisms of their plant communities on soil properties need to be determined to help evaluate the soil nutrient balance and predict the sustainability of restoration (Song et al., 2022; Liao et al., 2023). The Loess Plateau of China, which covers an area of about 64×10^4 km^2, has characterized by severe soil erosion and excessive desertification (Zheng, 2006; Zhang et al., 2018a). The Chinese government has undertaken a series of ecological restoration projects such as returning farmland to forest and grassland (Fu et al., 2000), which is an important measure to increase vegetation coverage and prevent fragmentation and degradation of ecosystem (Lozano et al., 2014; Zhang et al., 2016). After the converting of farmland into forest and grassland, secondary succession without human disturbance, biodiversity, and soil ecosystem functions have been significantly improved. Meanwhile, soil physical-chemical properties (Qiu et al., 2022), microbial community dynamics (Liu et al., 2022), soil enzyme activities (Chen et al., 2022), plant community composition (Zhu et al., 2021a), and plant diversity (Zhang, 2005) have been significantly changed. However, there are few researches on the variability of Leguminosae on soil physical-chemical properties and biological properties. In this study, we investigated the dynamic plant community composition, plant diversity, soil physical-chemical properties, and soil biological properties using different years of secondary successional abandoned cropland and farmland as the subjects. We hypothesized that plant community composition and plant diversity

would affect soil physical-chemical properties and soil biological properties to different degrees with succession time. In addition, we further hypothesized that Leguminosae are the dominant species in the plant community and have a greater influence on soil properties during secondary succession. Therefore, we focused on: (1) effects of succession time on plant community composition, species diversity, soil physical-chemical properties, and soil biological properties; (2) effects of plant community characteristics and community composition on soil properties; and (3) effects of Leguminosae on soil properties.

2 Materials and methods

2.1 Study area

A field experiment was conducted in the Zhifanggou watershed of Ansai District (36°42′–36°47′N, 109°13′–109°16′E), Shaanxi Province, northwestern China, which is in the center of the Loess Plateau. The soil in this area is classified by the Food and Agriculture Organization (FAO) as extremely erodible Calcaric Cambisol that developed from wind-blown loess deposits. Due to long-term wind-blown deposits and soil erosion, the catchment (8.73 km^2) has the typical landforms of the loess hilly and gully landscape with slope gradients varying from 0° to 65°, and altitudes ranging from 1000 to 1300 m a.s.l. (Wang et al., 2009). Climate in this region is classified as temperate with an average annual precipitation of 510 mm, of which approximately 70% falls between June and September (Zhang et al., 2016). The average frost-free period in this catchment is >150 d and the annual average temperature is 8.8°C, with the maximum temperature of 36.8°C in August and the minimum temperature of –23.6°C in January. The Zhifanggou watershed serves as a template for remedying soil erosion and ecological environment. In 1973, the Chinese government began to carry out the integrated management of soil and water conservation and vegetation restoration. One of the most widely used methods to prevent soil nutrient loss is to convert former farmlands into abandoned grassland for natural recovery without anthropogenic interference (Zhang et al., 2016). After decades of this artificial restoration, vegetation coverage in the area increased significantly, and large-scale herbaceous communities formed, which included the species *Artemisia sacrorum* Ledeb., *Lespedeza dahurica* Schindler, *Artemisia scoparia* Waldst. et Kit., and *Heteropappus altaicus* (Willd.) Novopokr. In addition, there are still a handful of farmlands in the gentle slope zone where maize, potatoes, and foxtail millet have been planted.

2.2 Experimental design

This study used the space-for-time substitution method, which has been applied to numerous field studies (Walker et al., 2010; Williams et al., 2013; Zhang et al., 2016; Zhang et al., 2018b) and a meta-analysis (Zhou et al., 2017) to investigate the effects of natural succession on the above- and below-ground ecosystem. Through a comprehensive field survey of the Zhifanggou watershed in Ansai District, four plots were selected. Farmlands that had been abandoned 5, 10, 18, and 30 a were randomly chosen from areas with similar gradients, slopes, and altitudes. Active farmland was used as the control (CK). Detailed information about each succession sequence of abandoned farmland and referential farmland is presented in Table S1. All selected sample plots had been plowed every spring before abandonment, and were planted mainly with maize and cereals, with minimal fertilizer application and irrigation relying mainly on rainfall. There was no human disturbance during the abandonment period and vegetation was naturally colonized and growing. Each succession sequence of the abandoned farmland was represented by three independent replicates and space between any two sites was large enough to exclude spatial dependence (<14 m) for the vast majority of soil and plant variables (Marriott et al., 1997). Three replicated plots (30 m×30 m; Fig. 1) were randomly set up in each plot for subsequent investigation and sampling. For each variable, average value of the three replicates in the same plot was taken to constitute observations. Thus, in total, 15 observations were established (5 succession sequences×3 replicates) for each variable.

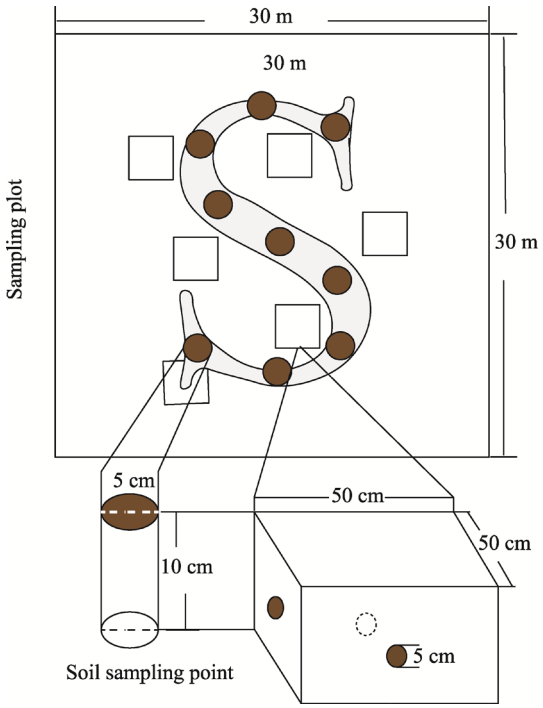

Fig. 1 Sampling process of the Zhifanggou watershed in the Loess Plateau, China

2.3 Vegetation investigation and soil sampling

Vegetation investigation and soil sampling were conducted in August 2022. Nine replicated sample points were selected along an "S" shape in each plot for soil sampling (Fig. 1). After removing the litter horizons and biological crusts, nine soil samples of 0–10 cm depth were collected from each point using a 5-cm diameter stainless steel auger, then fully homogenized to provide one composite sample per plot. These soil samples were immediately sieved through <2 mm mesh to remove visible litter, animal residue, roots, stones, and debris. Part of each soil sample was immediately taken back to the laboratory and stored at 4°C for biological characteristics analysis, and other subsamples were air-dried and stored at room temperature for physical-chemical analysis. Soil water content (SWC) and bulk density (BD) were obtained randomly from six points per plot using a 5-cm diameter steel core sampler (Fig. 1), then dried at 105°C to constant weight.

Vegetation characteristics were investigated *in situ*, and 10 quadrats with an area of 1 m^2 were randomly arranged in each plot to record the name, height, coverage, frequency, and density of each species. Plant coverage was estimated at each plot. Both above- and below-ground parts of all plants in each 1 m×1 m quadrat were collected by clipping and digging, respectively. After washing the roots with tap water, both above- and below-ground parts of all plants were dried at 75°C to constant weight to calculate above-ground biomass (AB) and below-ground biomass (BB). The species importance value (IV), Margalef richness index (M), Shannon-Wiener diversity index (H), and Pielou evenness index (E) were calculated (Zhang, 2005; Zhang et al., 2016):

$$\text{IV}=(\text{relative density}+\text{relative frequency}+\text{relative coverage}+\text{relative height})/4\times100\%, \quad (1)$$

where relative density (%), relative frequency (%), relative coverage (%), and relative height (%) are defined as the percentages of density, frequency, coverage, and height of a single species to the total density, frequency, coverage, and height of all species per plot, respectively.

$$M=(S-1)/\ln N, \quad (2)$$

$$H = -\sum_{i=1}^{S}(p_i \ln p_i), \tag{3}$$

$$E = -\sum_{i=1}^{S}(p_i \ln p_i)/\ln S, \tag{4}$$

where S is the total number of species in each plot; N is the sum density of all species in each plot; and P_i is the density proportion of species i.

2.4 Soil physical-chemical properties analysis

Soil organic carbon (SOC) concentration was measured using $K_2Cr_2O_7$ oxidation method (Bao, 2000). Soil total nitrogen (TN) concentration was determined using a continuous flow analyzer (AA3, Bran+Luebbe, Norderstedt, Germany) after micro-Kjeldahl digestion (Zhang et al., 2016). Concentrations of ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) of the soil were determined using a continuous flow analyzer (AA3, Bran+Luebbe, Norderstedt, Germany) after extractions of fresh soil with 2 M KCl for 18 h (Zhang et al., 2016). Soil total phosphorus (TP) concentration was analyzed using Mo-Sb anti-Spectro photograohy method (Bao, 2000) and soil available phosphorus (AP) was determined by Olsen method (Olsen et al., 1982). Soil alkaline phosphatase (ALP), urease (URE), catalase (CAT), and saccharase (SAC) activities were determined using the method described in previous study (Zhang et al., 2018b), which is shown in Table S2. Soil microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) were estimated from fresh soil samples using a chloroform fumigation-extraction method (Bao, 2000; Ren et al., 2016a). SWC was determined by oven drying samples at 105°C to constant weight (Bao, 2000). Soil pH was measured using a pH meter (Sartorius PB-10, Goettingen, Germany) after vibrating soil-water (1:5) suspension for 30 min (Ren et al., 2017; Zhang et al., 2018b). Soil BD was determined using soil core method, and obtained by calculating the ratio of soil mass to total volume after oven-drying at 105°C to constant weight (Ren et al., 2016b). Soil temperature was measured using a right-angle geothermometer. Soil clay was determined by a laser particle size analyzer.

2.5 Soil microbial respiration and metabolic quotient measurement

Soil microbial respiration was routinely determined using alkali (NaOH) absorption method as described by both Hu et al. (1997) and Liu et al. (2010). Briefly, 25 g of fresh soil was weighed from each plot and placed evenly in a 500-mL glass flask. The blank treatments (without soil) were used as controls. A 25-mL flask with 10 mL 0.5 mol/L NaOH solution was placed in the 500 mL glass flask to capture CO_2 evolved from the soil. There apparatuses were incubated at 25°C in the darkness for two weeks, and cover of each flask was opened for half an hour once a day in previous week and once every two days in the next week. Soil microbial metabolic quotient (qCO_2) was calculated as MR/MBC (where MR is microbial respiration) (Wardle and Ghani, 1995).

2.6 Statistical analyses

Distribution of all data was checked using Shapiro-Wilk test, and all variables were found to follow a normal distribution. One-way analysis of variance (ANOVA) and Duncan's multiple range test (P<0.05) were used to assess the effects of successional stage on plant community composition, plant species diversity, soil physical-chemical properties, and soil biological activity using R v.3.1.3 software (R Core Team, 2015). Correlations between plant characteristics, soil physical-chemical properties, and soil biological activity were identified using redundancy analysis (RDA) and relative interpretation rate of vegetation characteristics on soil properties. Venn diagram analysis of relative interpretation rates of Leguminosae dominant species on soil physical-chemical and biological properties was undertaken. The clustering of different samples along successional stage by variables of soil and plant characteristics were revealed through nonmetric multidimensional scaling (NMDS) method. Both RDA and NMDS were conducted by CANOCO v.5.0 software package (Ter Braak and Smilauer, 2002). Analysis of interpretation rate

of Leguminosae dominant species with soil physical-chemical and biological properties used Venn diagram package at R v.4.2.1.

3 Results

3.1 Changes in plant community characteristics

Vegetation characteristics changed significantly with successional time (Table 1). Plant community coverage, AB, and BB increased rapidly at 5 a plot, decreased at 10 a plot, and significantly increased again from 10 to 30 a plot (Table 1). Plant community coverage, AB, and BB varied from 40.44% to 58.94%, 116.12 to 275.06 g/m^2, and 44.58 to 117.54 g/m^2, respectively, and the minimum and maximum values occurred at 10 and 30 a plots, respectively (Table 1). The *M*, *H*, and *E* significantly increased with succession time, ranging from 1.62 to 3.51, 1.13 to 3.65, and 0.47 to 0.95, respectively (Table 1).

Table 1 Plant community characteristics over different successional time

Index	Years of farmland abandonment				*F*	*P*
	5 a	10 a	18 a	30 a		
Coverage (%)	58.87±3.82^a	40.44±2.47^c	51.59±2.61^b	58.94±1.70^a	30.04	<0.001
Above-ground biomass (g/m^2)	145.99±5.97^c	116.12±8.04^d	228.27±16.27^b	275.06±8.53^a	147.06	<0.001
Below-ground biomass (g/m^2)	52.46±4.53^c	44.58±4.08^c	91.87±7.15^b	117.54±8.21^a	90.34	<0.001
Margalef richness index	1.62±0.08^c	2.67±0.27^b	2.92±0.27^b	3.51±0.09^a	48.17	<0.001
Shannon-Wiener diversity index	1.13±0.07^d	2.50±0.13^c	2.89±0.29^b	3.65±0.12^a	114.38	<0.001
Pielou evenness index	0.47±0.03^d	0.65±0.02^c	0.80±0.03^b	0.95±0.02^a	227.99	<0.001

Note: Different lowercase letters within the same row indicate significant difference among different successional time at P<0.05 level. Mean±SD; n=3.

Plant community composition was considerably affected with succession time (Table 2), and NMDS suggested that sampling plots were clearly gathered into four well-differentiated groups at plant community level (Fig. S1). IV of *Artemisia capillaris* Thunb. significantly decreased with succession time, and plant species dominated the community at 5 and 10 a plots and turned into a companion species for those plots abandoned for more than 18 a. Although *H. altaicus* was also the dominant species at 5 a plot, its dominance was replaced by *Stipa bungeana* Trin. that appears at 10 a plot and was not present at 30 a plot. IV of *L. dahurica* was significantly increased during the first 18 a of abandonment, was decreased at 30-a plot, and dominated the plant community at 18–30 a plot. Two perennial species, *A. sacrorum* and *Artemisia giraldii* Pamp., appeared over the course of succession at 10 a plot, and were dominant species at 18 and 30 a plots, respectively. In general, dominant species of plant community appeared to gradually transition from *A. capillaris* and *H. altaicus* to *L. dahurica*, *A. sacrorum*, and *A. giraldii* during 30 a of abandonment. For plant species composition, IV of Compositae plants decreased rapidly during the first 18 a of abandonment and then increased at 30 a plot, with the lowest point at 18 a plot (31.10%) and the peak at 5 a plot (54.09%). IV of Gramineae plants significantly increased and then decreased with succession time, and the peak occurred at 18 a plot (29.43%). IV of Leguminosae plants significantly increased with successional time, ranging from 9.86% to 36.49%.

3.2 Changes in soil physical-chemical properties

NMDS revealed that soil physical-chemical properties significantly changed with successional time (Fig. S2). SOC and soil clay was significantly increased, ranging from 3.53 to 5.70 g/kg and 18.86% to 20.81% for farmland and 30 a plot, respectively (Fig. 2; Table 3). Compared with farmland, SWC, TN, NH_4^+-N, and NO_3^--N contents were significantly lower at 5 a plot but significantly higher with successional time and rising to farmland levels at 10 a plot (Table 3). SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay contents reached their highest values at 30 a plot, and were 61.47%, 45.51%, 13.11%, 65.32%, 36.23%, and 10.34% higher than those at farmland,

respectively (Table 3). BD, soil temperature, TP, and AP values were higher at farmland than at those plots, and decreased significantly with increasing successional time, ranging from 1.15 to

Table 2 Importance value of plant species over different successional time

Plant species	Years of farmland abandonment			
	5 a	10 a	18 a	30 a
	(%)			
Patrinia heterophylla Bunge	-	4.56±0.49^{a}	1.89±0.26^{b}	0.58±0.09^{c}
Dracocephalum moldavica L.	4.03±0.48^{a}	-	-	-
Lespedeza dahurica Schindler	9.86±0.11^{d}	16.36±0.66^{c}	21.20±0.53^{a}	17.79±0.40^{b}
Medicago sativa L.	-	-	3.56±0.44^{b}	6.53±0.57^{a}
Vicia sepium L.	-	-	2.33±0.51^{a}	-
Thermopsis lanceolata R. Br.	-	-	-	3.07±0.64^{a}
Glycyrrhiza uralensis Fisch.	-	-	1.22±0.39^{a}	-
Astragalus melilotoides Pall.	-	3.89±0.28^{b}	2.98±0.62^{b}	6.11±0.46^{a}
Gueldenstaedtia verna Boriss.	-	-	-	2.99±0.34^{a}
Setaria viridis (L.) Beauv.	10.29±0.36^{a}	5.36±0.46^{b}	0.68±0.06^{c}	-
Poa pratensis L.	6.41±0.27^{a}	2.09±0.15^{c}	3.30±0.33^{b}	-
Stipa bungeana Trin.	-	19.41±0.77^{a}	13.45±0.99^{b}	8.60±0.79^{c}
Cleistogenes chinensis (Maxim.) Keng	-	-	2.50±0.58^{a}	0.55±0.36^{b}
Roegneria kamoji Ohwi	-	-	4.54±0.50^{a}	0.30±0.11^{b}
Phragmites australis (Cav.) Trin.ex Steud	-	-	-	0.75±0.18^{a}
Leymus secalinus (Georgi) Tzvel.	-	-	-	1.41±0.13^{a}
Bothriochloa ischaemum (Linnaeus) Keng	-	-	4.96±0.65^{b}	12.74±0.64^{a}
Viola philippica Cav.	-	1.21±0.27^{a}	-	-
Artemisia capillaris Thunb.	35.02±0.44^{a}	18.31±0.78^{b}	3.68±0.18^{c}	2.07±0.76^{d}
Heteropappus altaicus (Willd.) Novopokr	17.37±0.80^{a}	8.29±0.74^{b}	2.17±0.44^{c}	-
Cirsium setosum (Willd.) MB.	1.70±0.14^{a}	-	-	-
Artemisia sacrorum Ledeb.	-	7.83±0.72^{c}	16.49±0.90^{a}	10.11±0.62^{b}
Ixeris polycephala Cass.	-	2.30±0.38^{a}	-	1.84±0.32^{a}
Saussurea japonica (Thunb.) DC.	-	-	2.59±0.25^{a}	1.23±0.25^{b}
Artemisia giraldii Pamp.	-	2.24±0.21^{c}	5.12±0.55^{b}	18.88±0.93^{a}
Ixeridium sonchifolium (Maxim.) Shih	-	1.59±0.13^{a}	-	0.50±0.12^{b}
Bidens parviflora Willd.	-	-	1.05±0.09^{a}	-
Salsola collina Pall.	4.87±0.06^{a}	1.24±0.26^{b}	-	0.85±0.11^{c}
Chenopodium glaucum L.	-	2.79±0.78^{a}	-	-
Potentilla discolor Bge.	6.99±0.61^{a}	2.53±0.47^{b}	-	-
Duchesnea indica (Andr.) Focke	-	-	3.37±0.43^{a}	-
Polygala tenuifolia Willd.	1.17±0.33^{b}	-	0.57±0.06^{c}	1.86±0.10^{a}
Incarvillea sinensis Lam.	2.29±0.20^{a}	-	2.34±0.38^{a}	1.26±0.06^{b}
Compositae	54.09±0.66^{a}	40.57±0.21^{b}	31.10±0.38^{d}	34.63±0.22^{c}
Gramineae	16.70±0.44^{d}	26.86±0.17^{b}	29.43±1.22^{a}	24.35±0.26^{c}
Leguminosae	9.86±0.11^{d}	20.25±0.93^{c}	31.30±1.62^{b}	36.49±0.08^{a}
Sum of Compositae, Gramineae, and Leguminosae	80.65±0.70^{d}	87.67±1.27^{c}	91.82±0.63^{b}	95.48±0.59^{a}

Note: Different lowercase letters within the same row indicate significant difference among different successional time at $P<0.05$ level. Mean±SD; $n=3$. - means no value.

1.29 g/cm^3, 16.44°C to 18.71°C, 0.53 to 0.60 g/kg, and 0.61 to 1.95 mg/kg, respectively (Table 3). In addition, soil pH was slightly higher at all plots than at farmland, although there was no statistical difference between plots (Table 3).

RDA showed that soil physical-chemical properties were significantly correlated with vegetation characteristics and plant community composition (Fig. 3). For vegetation characteristics, the first two axes significantly explained 96.37% of all considered variables, indicating that *M*, *H*, *E*, AB, BB, Leguminosae, Gramineae, Compositae and sum of Leguminosae, Gramineae, and Compositae were positively correlated with SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay, and negatively correlated with TP, AP, BD, and soil temperature (Fig. 3a). Conversely, Compositae plants were negatively correlated with SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay, and positively with TP, AP, BD, and soil temperature. For plant community composition, the first two axes explained 75.68% of all considered variables, and SWC, AP, NH_4^+-N, and NO_3^--N were

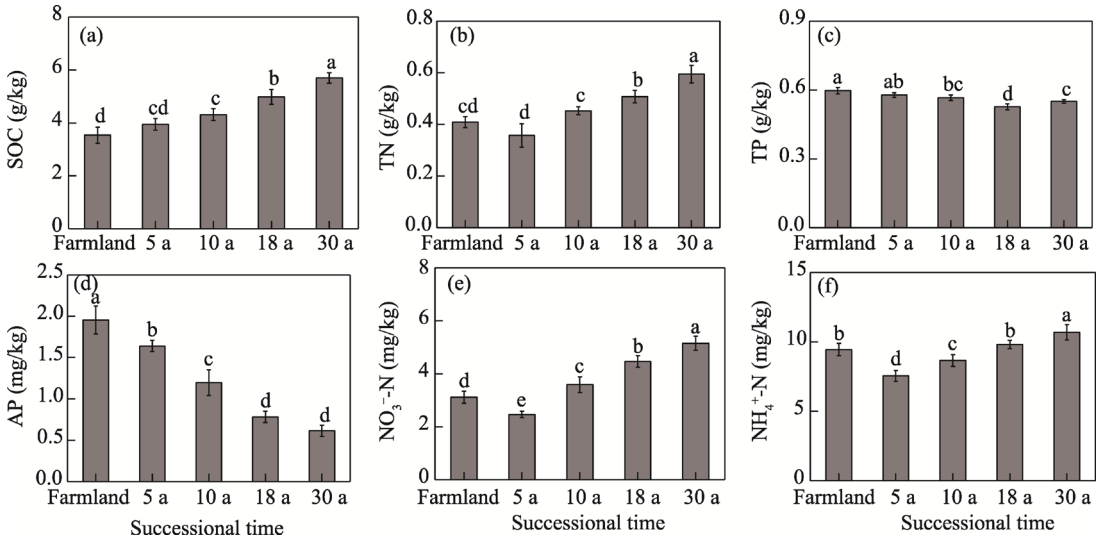

Fig. 2 Changes of soil nutrient contents over different successional time. (a), soil organic carbon (SOC); (b), total nitrogen (TN); (c), total phosphorus (TP); (d), available phosphorus (AP); (e), nitrate nitrogen (NO_3^--N); (f), ammonium nitrogen (NH_4^+-N). Different lowercase letters indicate significant difference among different successional time at $P<0.05$ level. Bars are standard errors.

Table 3 Soil physical-chemical properties over different successional time

Parameter	Farmland	Years of farmland abandonment				*F*	*P*
		5 a	10 a	18 a	30 a		
Soil water content (%)	7.24±0.18^e	6.71±0.16^d	7.82±0.13^c	9.28±0.26^b	9.86±0.10^a	177.30	<0.001
pH	8.49±0.02^c	8.54±0.03^{bc}	8.62±0.02^a	8.49±0.03^c	8.56±0.03^b	10.72	0.001
Soil bulk density (g/cm^3)	1.29±0.02^a	1.26±0.02^a	1.21±0.03^b	1.18±0.02^{bc}	1.15±0.02^c	23.30	<0.001
Soil temperature (°C)	18.71±0.24^a	18.14±0.13^b	17.52±0.30^c	16.44±0.26^d	17.56±0.32^c	32.16	<0.001
Clay (%)	18.86±0.81^c	19.22±0.28^c	19.52±0.26^{bc}	20.19±0.33^{ab}	20.81±0.29^a	9.21	0.002
SOC (g/kg)	3.53±0.31^d	3.94±0.22^{cd}	4.31±0.23^c	4.98±0.28^b	5.70±0.20^a	35.28	<0.001
TN (g/kg)	0.41±0.02^{cd}	0.36±0.05^d	0.45±0.02^c	0.51±0.02^b	0.59±0.03^a	32.47	<0.001
TP (g/kg)	0.60±0.01^a	0.58±0.01^{ab}	0.57±0.01^{bc}	0.53±0.01^d	0.55±0.01^c	14.43	<0.001
NH_4^+-N (mg/kg)	9.45±0.44^b	7.56±0.38^d	8.66±0.42^c	9.82±0.30^b	10.68±0.56^a	23.13	<0.001
NO_3^--N (mg/kg)	3.12±0.23^e	2.47±0.12^d	3.59±0.29^c	4.47±0.21^b	5.15±0.26^a	63.54	<0.001
AP (mg/kg)	1.95±0.17^a	1.64±0.07^b	1.20±0.16^c	0.78±0.07^d	0.61±0.07^d	69.98	<0.001

Note: SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus. Different lowercase letters within the same row indicate significant difference among different successional time at $P<0.05$ level. Mean±SD; $n=3$.

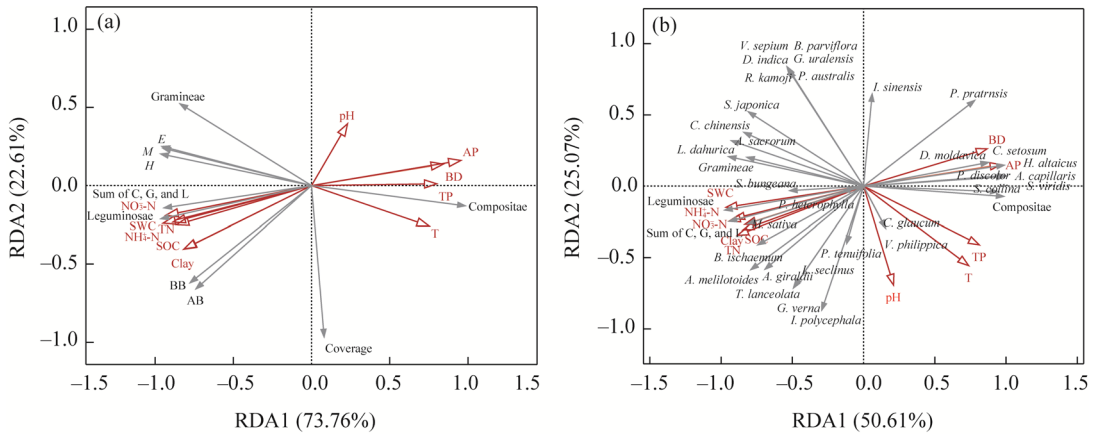

Fig. 3 Redundancy analysis (RDA) for the relationships among soil physical-chemical properties, vegetation characteristics, and plant community composition. (a), relationships between soil physical-chemical properties (red arrows) and vegetation characteristics (grey arrows); (b), relationships between soil physical-chemical properties (red arrows) and plant community composition (grey arrows). SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; SWC, soil water content; BD, bulk density; T, soil temperature; *M*, Margalef richness index; *H*, Shannon-Wiener diversity index; *E*, Pielou evenness index; AB, above-ground biomass; BB, below-ground biomass; sum of C, G, and L, sum of Compositae, Gramineae, and Leguminosae.

the most influential factors causing the changes in plant composition, contributing to 48.40%, 47.80%, 46.70%, and 44.20% of total variation (Fig. 3b).

3.3 Changes in soil biological properties and responses to plant community characteristics

Four soil enzymatic activities (SAC, URE, ALP, and CAT) responded consistently with successional time (Figs. 4a–d and S3). Notably, the activities of four soil enzymes were significantly higher at abandoned lands than at farmland, with the increased rates ranging from 25.46% to 292.19% (SAC), 38.08% to 112.34% (URE), 39.02% to 211.12% (ALP), and 4.23% to 21.37% (CAT), respectively. All four soil enzymatic activities increased significantly with successional time and reached their maximum values at 30 a plot. Similarly, MBC and MBN significantly increased with successional time, with growth rates ranging from 26.33% to 156.55% and from 17.58% to 116.79% for farmlands and 30 a plot, respectively (Fig. 4e and f). Soil microbial respiration increased and peaked at 10 a plot and then sharply decreased with successional time (Fig. 4g). Soil respiration at abandoned lands was higher than that at farmland (Fig. 4g). Value of qCO_2 increased significantly at 5 a plot compared with farmland, then dramatically decreased with successional time (Fig. 4h). In addition, values of qCO_2 at 18 and 30 a plots were significantly lower than those at farmland, 5, and 30 a plots.

RDA showed a significant correlation between soil biological properties and plant community characteristics (Fig. 5). For vegetation characteristics, the first two axes significantly explained 93.37% of all considered variables (Fig. 5a). In particular, Leguminosae plants were the most important factor, contributing 81.60% of total variation. RDA indicated that *M*, *H*, *E*, AB, BB, Leguminosae, Gramineae, and total of Leguminosae, Gramineae, and Compositae were positively correlated with MBC, MBN, SAC, URE, ALP, and CAT and negatively correlated with qCO_2 (Fig. 5a). Conversely, Compositae plants were negatively correlated with MBC, MBN, SAC, URE, ALP, and CAT, and positively correlated with qCO_2 (Fig. 5a). In addition, all plant community composition variables significantly explained 78.83% of total soil biological variation (Fig. 5b).

3.4 Effect of Leguminosae on soil physical-chemical properties and biological characteristics

RDA showed that Leguminosae had the greatest influence on soil physical-chemical properties, with a relative explanation percentage of 75.90%, which was significantly higher than other vegetation characteristics (Table 4). Moreover, RDA showed that Leguminosae had the greatest

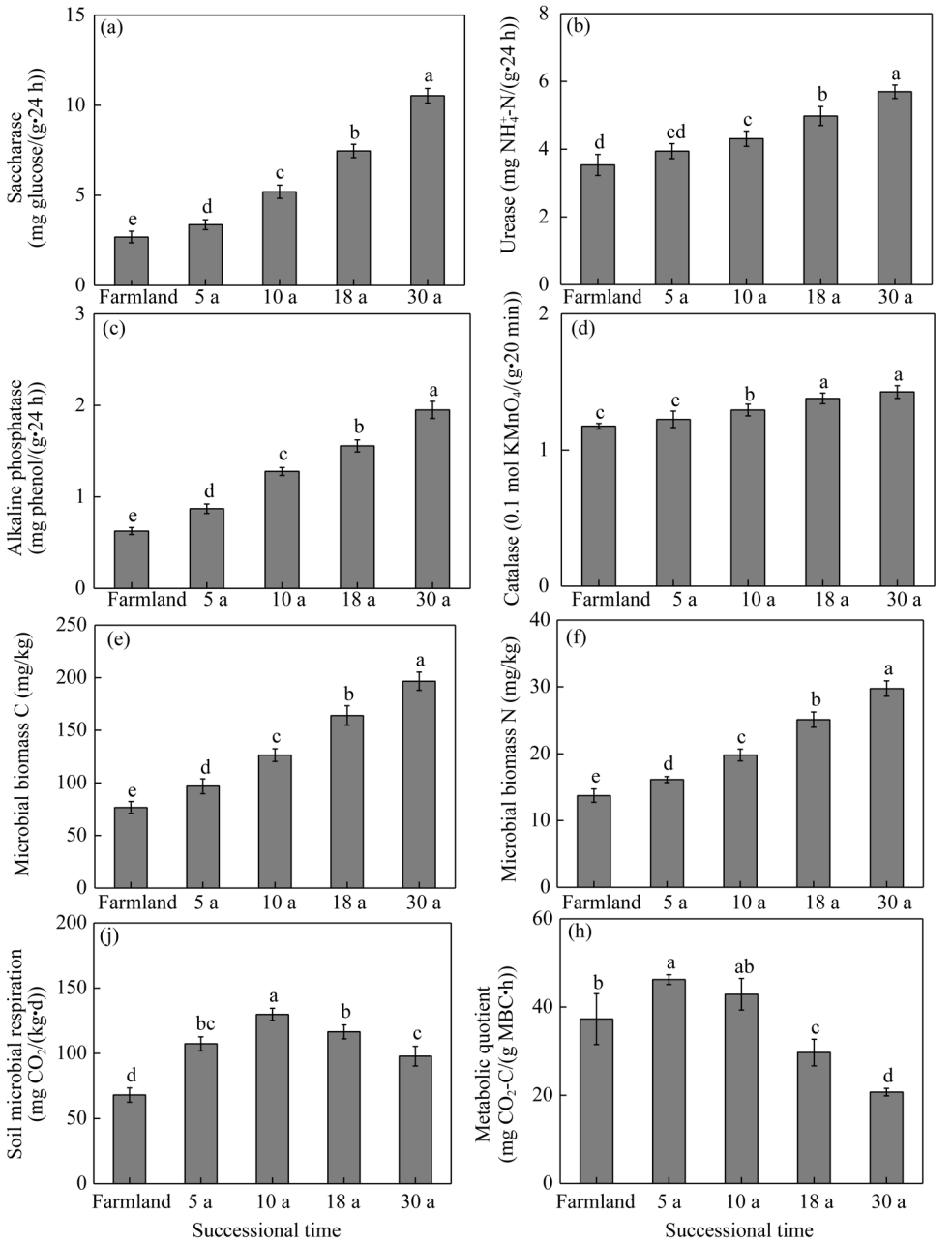

Fig. 4 Changes of soil biological properties over different successional time. Different lowercase letters indicate significant difference among different successional time at $P<0.05$ level. Bars are standard errors. C, carbon; N, nitrogen. (a), saccharase; (b), urease; (c), alkiline phosphatase; (d), catalase; (e), microbial biomass C (MBC); (f), microbial biomass N; (g), soil microbial respiration; (h), metabolic quotient.

influence on soil biological properties, with a relative explanation percentage of 81.60%, which was significantly higher than other vegetation characteristics (Table 5). Among plant community compositions, Leguminosae were the most dominant community, with the most dominant species *Medicago sativa* L. making the greatest relative contribution to soil physical-chemical and biological properties with 10.60% and 36.90%, respectively (Fig. 6). In summary, Leguminosae plants can be regarded as the most important plant factors associated with soil physical-chemical and biological properties, but not dominant species and species diversity.

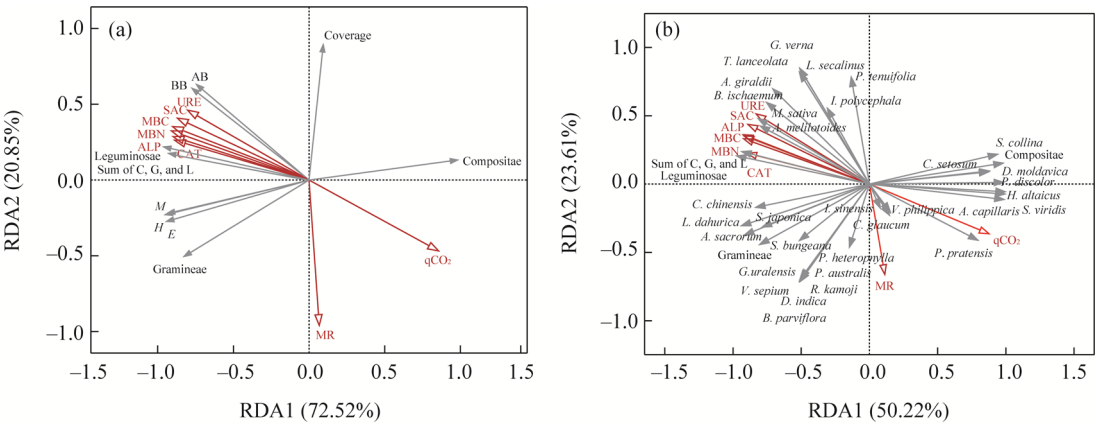

Fig. 5 Redundancy analysis (RDA) for relationship among soil biological properties, vegetation characteristics, and plant community composition. (a), relationships between soil biological properties (red arrows) and vegetation characteristics (grey arrows); (b), relationships between soil biological properties (red arrows) and plant community composition (grey arrows); MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; ALP, alkaline phosphatase; URE, urease; CAT, catalase; SAC, saccharase; MR, microbial respiration; qCO_2, metabolic quotient; *M*, Margalef richness index; *H*, Shannon-Wiener diversity index; *E*, Pielou evenness index; AB, above-ground biomass; BB, below-ground biomass; sum of C, G, and L, sum of importance values of Compositae, Gramineae, and Leguminosae plants.

Table 4 Effects of vegetation characteristics on soil physical-chemical properties over successional time

Parameter	Contribution (%)	*F*	*P*
Leguminosae	75.90	27.4	0.002
Compositae	66.10	17.6	0.002
Gramineae	37.90	5.8	0.016
Above-ground biomass	59.40	13.4	0.004
Below-ground biomass	59.10	13.3	0.002
Margalef richness index	53.30	10.6	0.002
Shannon-Wiener diversity index	58.30	12.9	0.002
Pielou evenness index	56.20	11.8	0.002

Table 5 Effects of vegetation characteristics on soil biological properties over successional time

Parameter	Contribution (%)	*F*	*P*
Leguminosae	81.60	31.6	0.002
Compositae	59.00	13.6	0.006
Gramineae	27.30	3.6	0.052
Above-ground biomass	73.70	25.8	0.004
Below-ground biomass	77.70	31.8	0.002
Margalef richness index	45.10	7.9	0.020
Shannon-Wiener diversity index	47.60	8.4	0.004
Pielou evenness index	46.60	8.4	0.010

4 Discussion

4.1 Plant characteristics over successional time

A. capillaris, an annual species belonging to Compositae, was a pioneer species that first colonized the bare farmland and quickly became the dominant species at 5 a plot (Table 2). The

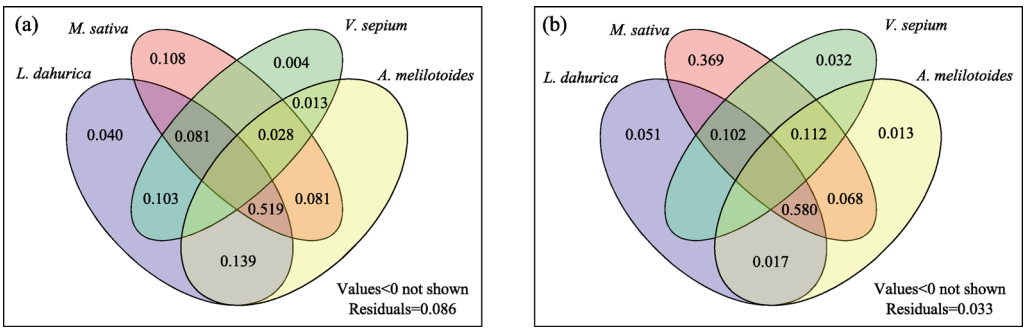

Fig. 6 Variance partitioning analysis of dominant species of Leguminosae on soil physical-chemical properties (a) and soil biological properties (b)

strong resource competitiveness and rapid environmental adaptability led to rapid growth of *A. capillaris* and further inhibited the growth of other species (Zhang et al., 2016), resulting in low *H*, *M*, and *E* at 5 a plot (Table 1). This study showed that *H*, *M*, and *E* significantly increased with successional time until 30 a plot (Table 1), and more species had appeared in 18 and 30 a plots, such as *S. bungeana*, *A. sacrorum*, and *Astragalus melilotoides* Pall. (Table 2). Similar results were found in previous studies, with high species diversity and richness occurring during middle successional stage of the Chinese Loess Plateau (25 a of abandonment) (Wang et al., 2009; Zhang et al., 2016; Sun et al., 2017). The colonization by plants improved soil conditions and provided more living space for more species during secondary succession (Zhu et al., 2021b; Wang et al., 2022), and the improvement in soil condition could be demonstrated by increased SWC and clay content and decreased BD and pH (Table 3). At the same time, many species of different ecotypes interacted with each other to reach a stable state in these improved community environments (Liu et al., 2023; Yang et al., 2023), thereby causing an increase in species diversity and richness (Sun et al., 2022; Gu et al., 2023; Kong et al., 2023). In addition, the results showed that IV of Leguminosae and Gramineae plants increased with successional time (Table 2), indicating that these families are more adaptable to the arid environment of the Loess Plateau than others (Zhang et al., 2021; Liu et al., 2022). For example, Leguminosae have deeper roots to obtain water and nutrients (Hu et al., 2016). Morever, *M*, *H*, and *E* were found to be positively correlated with Leguminosae and Gramineae plants (Figs. 3, 5, and S2). It should be noted that strong C and N fixation capacity of Gramineae and Leguminosae plants can increase soil C and N input to improve availability (Hu et al., 2016; Tian et al., 2016), thereby creating suitable conditions for plant colonization to increase species diversity and richness. In contrast, Gramineae and Leguminosae plants can coexist with other species due to complementarity, facilitation, and niche differentiation (HilleRisLambers et al., 2004; Wu et al., 2017), resulting in increased species diversity and richness. However, Compositae plants can inhibit the growth of other species due to allelopathic effects (Baličević et al., 2016), leading to them being negatively correlated with *M*, *H*, and *E* (Figs. 3 and 5). Above all, these results validate the hypothesis that plant community composition and species diversity significantly changed with successional time.

4.2 Responses of soil physical-chemical and biological properties to plant community characteristics

Soil physical properties are sensitive to alterations in plant characteristics (e.g., population composition, species diversity, and biomass) (Ile et al., 2021; Cotrufo et al., 2022). The results indicated that dynamics of plant diversity (*M*, *H*, and *E*) and coverage corresponded to the accumulation of above- and below-ground biomass (Table 1), with both being related to SWC, BD, soil temperature, and clay (Fig. 3a). This result showed that secondary succession of plant communities can alter soil physical properties (Jiao et al., 2011). First, the increase in above-ground biomass implies an improvement in vegetation and litter coverage (O'Halloran et al., 2013; DeBerry and Atkinson, 2014), thereby reducing solar radiation on the soil surface (Zhao

et al., 2015) and ultimately leading to an increase in SWC and a decrease in soil temperature with successional time (Table 3). Secondly, community composition changed from annual herbs to perennial Compositae, Leguminosae, and Gramineae plants (Table 2), and these species can reduce soil moisture loss (soil evaporation and plant transpiration) due to their degree of coverage and drought-tolerance (Jiao et al., 2011; Hu et al., 2016). Finally, accumulation of plant biomass could offer food sources to soil animals (Table 1), and disturbance by animals could decrease BD and increase soil clay content during secondary succession (Háněl, 2003; Jing et al., 2014). Ren et al. (2017) also found that plant diversity (*M*, *H*, and *E*) synchronously increased with soil microbial diversity and biomass during restoration, and that microbial dynamics could alter soil texture (e.g., BD and clay). However, pH changed more slowly with successional time than SWC, BD, soil temperature, and clay (Table 3), which is consistent with the results of previous studies (An et al., 2008; Zhang et al., 2016). This suggests that secondary succession of abandoned farmlands has little effect on soil pH, since pH is the result of multiple synergies between biotic and abiotic factors (Criquet et al., 2000).

In addition, our results showed that soil chemical properties (SOC, TN, TP, NH_4^+-N, NO_3^--N, and AP) were coupled to changes in plant diversity, coverage, AB, and BB (Fig. 3a). Not surprisingly, the colonization of plants fixes CO_2 from atmosphere through photosynthesis, and returns C to soil in the form of litter and rhizodeposition starting from the initial period of succession (Ohtsuka et al., 2010; Xiao et al., 2021). This cause SOC to increase significantly with successional time (Fig. 2a). In contrast to SOC, measures of TN, NH_4^+-N, NO_3^--N, TP, and AP decreased significantly at 5 a plot compared with farmland (Fig. 2b–f), which is attributable to the cessation of input from fertilizers and absorption by plants (Zhang et al., 2016). As above- and below-ground biomass gradually increased, contents of TN, NH_4^+-N, and NO_3^--N increased significantly with successional time (Fig. 2b, e, and f) due to the increase in Leguminosae plants with N-fixing capacity causing an increase in N content of plant-soil system (O'dea et al., 2015). P is a more 'rock-derived' element and is fixed only slowly from atmosphere (Huang et al., 2013), and continuous increase in above-ground biomass of plants will absorb a large amount of P from soil (Chen et al., 2000), causing significant decreases in TP and AP contents with successional time (Fig. 2c and d). Although soil nutrients declined at the early stage of succession to some extent, they rose to farmland levels at 10 and 18 a plots and exceeded farmland levels at 30 a plot (Fig. 2), indicating that soil nutrient status can be improved with successional time (Wang et al., 2009; Zhang et al., 2016). Net primary productivity of vegetation was enhanced during secondary succession (Table 1), causing increases in quantity of plant litter and dead roots, and ultimately improving soil nutrient levels (Peichl et al., 2012). Simultaneously, improving soil environment accelerated the decomposition of organic matter and then increased the accumulation of soil nutrients (Zhang et al., 2018b). Additionally, growth of plants controlled soil erosion, which also reduced losses of soil C, N, and P due to surface runoff (Zhu et al., 2021a; Luo et al., 2022).

Development of plant coverage and biomass is the foundation of soil restoration (Ren et al., 2017), and also strongly affects the dynamics of soil biological properties (Ren et al., 2016a). The results showed that soil enzymatic activities (SAC, URE, ALP, and CAT) and microbial biomasses (MBC and MBN) significantly increased with successional time (Figs. 4 and S3), and such alterations were also coupled to shifts in plant biomass and soil physical-chemical properties (Figs. 5 and 6). This indicated that secondary succession improves plant residues and soil microenvironment, and ultimately promotes soil biological activities. For example, increased plant residues during secondary succession contain a large amount of substrates that stimulate microbial growth and enzyme synthesis (Lucas-Borja et al., 2016). An improved soil environment (SWC, BD, and clay; Table 3) during secondary successional can promote the growth of microorganisms and contribute further to the development of microbial biomass and enzymatic activities (Yang et al., 2020; Guan et al., 2022). In addition, the development of below-ground biomass accelerates soil ventilation, promoting the release of exogenous enzymes by increasing rhizosphere exudates and ultimately altering microbial biomass and enzymatic activities (Zhang

et al., 2011; Zhang et al., 2018a). In contrast to microbial biomass and enzymatic activities, microbial respiration and qCO_2 increased significantly at 5 and 10 a plots compared with farmland but then decreased dramatically with successional time (Fig. 4g and h). As qCO_2 indicates the maintenance energy size of microbial communities and utilization efficiency of substrate, it is a sensitive index that reflects the influence of environmental factors on microbial activity (Liu et al., 2010). At early stage of succession, fast-growing vegetation requires a large quantity of nutrients, so microorganisms must accelerate fixation of nutrients to meet the vegetation's needs (Zhang et al., 2016). The results showed that qCO2 and microbial respiration increased when the rate of microbial turnover and energy consumption increased (Plaza et al., 2004; Zhang et al., 2011). As succession progresses, the reduced environmental stress (lower BD and higher SWC) increases microbial efficiency and decreases qCO_2 because microorganisms need to invest little energy on maintenance (Ren et al., 2018; Zhao et al., 2018). This allows the soil to retain sufficient active organic matter to maintain good properties and sustainable utilization potential (Liu et al., 2010; Ren et al., 2018).

4.3 Effects of plant community composition, species diversity, and dominant species on soil properties

Plant community composition can reflect varying quality and quantity of plant residues (litter and rhizodeposition) provided to the decomposers (Yahdjian et al., 2017), and may also cause diverse micro-environmental conditions (Kardol and Wardle, 2010). Such resultant shifts are related to sources and turnover of soil nutrients and ultimately alter soil physical-chemical and biological properties (Xiao et al., 2017). The results showed that plant community composition was more closely related to soil physical-chemical and biological properties than species diversity and dominant species (Figs. 3 and 5), and indicated that plant functional group can better reflect soil properties. Li et al. (2018) found that plant functional groups representing a class of plant species with similar physiological and biochemical characteristics (N fixation and C fixation), which is more capable of dominating nutrient feedback and circulation of ecosystem than single species (Wu et al., 2017; Chou et al., 2018). Previous research has also shown that plant functional group composition can affect soil environmental conditions and nutrient supply to determine species diversity (Chen et al., 2021; Sidlauskaite et al., 2022), therefore, it can better reflect the interactive relationships between vegetation and soil than species diversity. In addition, the results showed that Leguminosae plants were the most important plant community factor associated with soil physical-chemical and biological properties (Fig. 6). Leguminosae plants play important role in promoting soil C and N accumulation and mineralization due to their capacity for N_2-fixation by symbiotic root bacteria (Wu et al., 2017). Furthermore, Leguminosae plants contribute a net increase in litter N concentration due to their strong N fixation ability and low degree of N reuse from old leaves to new leaves (Li et al., 2012; Li et al., 2015). In addition, litter with higher N content contains more unstable complex, which is easily decomposed by microorganisms (Fanin and Bertrand, 2016; Zhang et al., 2018a; Zheng et al., 2021). Therefore, it can be concluded that Leguminosae plants promote the transfer of nutrients between plants and soil by accelerating the decomposition of litter, and increase the functional diversity and activity of soil microbial community by enhancing substrates inputs (Li et al., 2012; Hu et al., 2016). Increasing MBC and MBN and decreasing qCO_2 and microbial respiration over successional time confirmed the above deduction (Fig. 4). Fterich et al. (2014) also found that Leguminosae plants could increase soil organic matter and had positive effect on soil enzyme activity as well as C and N use efficiency of microorganisms. These variations in soil biological variables were significantly correlated with soil physical-chemical properties (Fig. 6), indicating that Leguminosae plants can change soil nutrients and environmental conditions by affecting soil microbial and enzyme activities. In contrast, co-improvement of soil physical-chemical and biological properties caused by legume species stimulates the development of mycorrhizal fungi, which strengthen plant nutrient absorption (Zhang et al., 2011), which lead to shifts in species diversity and plant community composition (Tables 1 and 2). Above all, plant functional composition can better reflect soil

physical-chemical and biological properties than species diversity and dominant species, with Leguminosae plant in particular being used to indicate the restoration status of vegetation and soil during secondary succession.

5 Conclusions

Plant communities transitioned from annual herbs to perennial species during 30 a of secondary succession. IV of Leguminosae and Gramineae significantly increased with successional time, whereas IV of Compositae significantly decreased. Moreover, plant community coverage, AB, and BB decreased at 10 a plot, and was then increased between 10 and 30 a plots, whereas species diversity significantly increased with successional time during first 18 a of secondary succession, then decreased at 30 a plot. Soil physical-chemical and biological properties (except TP and AP) significantly improved during secondary succession, even though some variables (e.g., TN, NH_4^+-N, NO_3^--N, and SWC) degraded at the early stages compared with farmland. Changes of plant community composition had greater effects on soil physical-chemical properties and biological properties than species diversity and dominant species. Particularly, Leguminosae plants were the most important factor affecting soil physical-chemical and biological properties, and therefore can be used as indicators for observing the restoration status of vegetation and soil during secondary succession. This study provides suitable planting species for better vegetation restoration during secondary succession in the Chinese Loess Plateau.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Conceptualization: ZHANG Wei; Methodology: SUN Lin, YU Zhouchang; Formal analysis: TIAN Xingfang, SHI Jiayi, ZHANG Ying; Writing - original draft preparation: ZHANG Wei, SUN Lin, YU Zhouchang; Writing - review and editing: FU Rong, LIANG Yujie.

References

An S, Zheng F, Zhang F, et al. 2008. Soil quality degradation processes along a deforestation chronosequence in the Ziwuling area, China. CATENA, 75(3): 248–256.

Baličević R, Ravlić M, Kleflin J, et al. 2016. Allelopathic activity of plant species from Asteraceae and Polygonaceae family on lettuce. Herbologia, 16(1): 23–30.

Bao S. 2000. Soil and Agricultural Chemistry Analysis. Beijing: China Agriculture Press, 11–12. (in Chinese)

Bao Y, Gao M, Luo D, et al. 2022. The influence of plant community characteristics in urban parks on the microclimate. Forests, 13(9): 1342, doi: 10.3390/f13091342.

Berg B. 2014. Decomposition patterns for foliar litter–A theory for influencing factors. Soil Biology and Biochemistry, 78: 222–232.

Chabrerie O, Laval K, Puget P, et al. 2003. Relationship between plant and soil microbial communities along a successional gradient in a chalk grassland in north-western France. Applied Soil Ecology, 24(1): 43–56.

Chen C R, Condron L M, Davis M R, et al. 2000. Effects of afforestation on phosphorus dynamics and biological properties in a New Zealand grassland soil. Plant and Soil, 220(1–2): 151–163.

Chen Y C, Li W P, You Y, et al. 2022. Soil properties and substrate quality determine the priming of soil organic carbon during

vegetation succession. Plant and Soil, 471(1–2): 559–575.

Chen Y X, Wei T X, Sha G L, et al. 2022. Soil enzyme activities of typical plant communities after vegetation restoration on the Loess Plateau, China. Applied Soil Ecology, 170: 104292, doi: 10.1016/j.apsoil.2021.104292.

Chen Z F, Xiong P F, Zhou J J, et al. 2021. Effects of plant diversity on semiarid grassland stability depends on functional group composition and dynamics under N and P addition. Science of the Total Environment, 799: 149482, doi: 10.1016/j.scitotenv.2021.149482.

Chou C B, Hedin L O, Pacala S W. 2018. Functional groups, species and light interact with nutrient limitation during tropical rainforest sapling bottleneck. Journal of Ecology, 106(1): 157–167.

Cotrufo M F, Haddix M L, Kroeger M E, et al. 2022. The role of plant input physical-chemical properties, and microbial and soil chemical diversity on the formation of particulate and mineral-associated organic matter. Soil Biology and Biochemistry, 168: 108648, doi: 10.1016/j.soilbio.2022.108648.

Criquet S, Farnet A M, Tagger S, et al. 2000. Annual variations of phenoloxidase activities in an evergreen oak litter: Influence of certain biotic and abiotic factors. Soil Biology and Biochemistry, 32(11–12): 1505–1513.

DeBerry J W, Atkinson R B. 2014. Aboveground forest biomass and litter production patterns in Atlantic white cedar swamps of differing hydroperiods. Southeastern Naturalist, 13(4): 673–690.

Fan H B, Wu J P, Liu W F, et al. 2015. Linkages of plant and soil C:N:P stoichiometry and their relationships to forest growth in subtropical plantations. Plant and Soil, 392(1–2): 127–138.

Fanin N, Bertrand I. 2016. Aboveground litter quality is a better predictor than belowground microbial communities when estimating carbon mineralization along a land-use gradient. Soil Biology and Biochemistry, 94: 48–60.

Fterich A, Mahdhi M, Mars M. 2014. The effects of *Acacia tortilis* subsp. *raddiana*, soil texture and soil depth on soil microbial and biochemical characteristics in arid zones of Tunisia. Land Degradation and Development, 25(2): 143–152.

Fu B J, Chen L D, Ma K M, et al. 2000. The relationships between land use and soil conditions in the hilly area of the loess plateau in northern Shaanxi, China. CATENA, 39(1): 69–78.

Gu Q, Yu Q, Grogan P. 2023. Cryptogam plant community stability: Warming weakens influences of species richness but enhances effects of evenness. Ecology, 104(1): 3842, doi: 10.1002/ecy.3842.

Guan H L, Fan J W, Lu X K. 2022. Soil specific enzyme stoichiometry reflects nitrogen limitation of microorganisms under different types of vegetation restoration in the Karst areas. Applied Soil Ecology, 169: 104253, doi: 10.1016/j.apsoil.2021.104253.

Háněl L. 2003. Recovery of soil nematode populations from cropping stress by natural secondary succession to meadow land. Applied Soil Ecology, 22(3): 255–270.

Hao J W, Chu L M. 2021. Vegetation types attributed to deforestation and secondary succession drive the elevational changes in diversity and distribution of terrestrial mosses in a tropical mountain forest in Southern China. Forests, 12(8): 961, doi: 10.3390/f12080961.

HilleRisLambers J, Harpole W S, Tilman D, et al. 2004. Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. Ecology Letters, 7(8): 661–668.

Horodecki P, Jagodzinski A M. 2017. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecology and Management, 406: 1–11.

Hu G Z, Liu H Y, Yin Y, et al. 2016. The role of legumes in plant community succession of degraded grasslands in northern China. Land Degradation and Development, 27(2): 366–372.

Hu S, van Bruggen A H C. 1997. Microbial dynamics associated with multiphasic decomposition of ^{14}C-labeled cellulose in soil. Microbial Ecology, 33(2): 134–143.

Huang W, Liu J, Wang Y P, et al. 2013. Increasing phosphorus limitation along three successional forests in southern China. Plant and Soil, 364(1–2): 181–191.

Ile O J, Aguilos M, Morkoc S, et al. 2021. Root biomass distribution and soil physical properties of short-rotation coppice American sycamore (*Platanus occidentalis* L.) grown at different planting densities. Forests, 12(12): 1806, doi: 10.3390/f12121806.

Jiao F, Wen Z M, An S S. 2011. Changes in soil properties across a chronosequence of vegetation restoration on the Loess Plateau of China. CATENA, 86(2): 110–116.

Jing Z, Cheng J, Jin J, et al. 2014. Revegetation as an efficient means of improving the diversity and abundance of soil eukaryotes in the Loess Plateau of China. Ecological Engineering, 70: 169–174.

Kardol P, Wardle D A. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. Trends in

Ecology & Evolution, 25(11): 670–679.

Kong Y S, Zhang H K, Tian L L, et al. 2023. Relationships between denitrification rates and functional gene abundance in a wetland: The roles of single- and multiple-species plant communities. Science of the Total Environment, 863: 160913, doi: 10.1016/j.scitotenv.2022.160913.

Li J, Liu Y, Hai X, et al. 2019. Dynamics of soil microbial C:N:P stoichiometry and its driving mechanisms following natural vegetation restoration after farmland abandonment. Science of the Total Environment, 693: 133613, doi: 10.1016/j.scitotenv.2019.133613.

Li J H, Jiao S M, Gao R Q, et al. 2012. Differential effects of legume species on the recovery of soil microbial communities, and carbon and nitrogen contents, in abandoned fields of the Loess Plateau, China. Environmental Management, 50(6): 1193–1203.

Li J W, Liu Y L, Hai X Y, et al. 2019. Dynamics of soil microbial C:N:P stoichiometry and its driving mechanisms following natural vegetation restoration after farmland abandonment. Science of the Total Environment, 693: 133613, doi: 10.1016/j.scitotenv.2019.133613.

Li Q, Song Y T, Li G D, et al. 2015. Grass-legume mixtures impact soil N, species recruitment, and productivity in temperate steppe grassland. Plant and Soil, 394(1–2): 271–285.

Li W, Zhang R, Liu S, et al. 2018. Effect of loss of plant functional group and simulated nitrogen deposition on subalpine ecosystem properties on the Tibetan Plateau. Science of the Total Environment, 631–632: 289–297.

Li X Y, Jin H J, He R X, et al. 2023. Impact of wildfire on soil carbon and nitrogen storage and vegetation succession in the Nanweng? The National Natural Wetlands Reserve, Northeast China. CATENA, 221: 106797, doi: 10.1016/j.catena.2022.106797.

Liao J J, Dou Y X, An S S. 2023. Plant community productivity is associated with multiple ecological stoichiometry in restoration grasslands. Ecological Engineering, 187: 106845, doi: 10.1016/j.ecoleng.2022.106845.

Liu H F, Liang C T, Ai Z M, et al. 2019. Plant-mycorrhizae association affects plant diversity, biomass, and soil nutrients along temporal gradients of natural restoration after farmland abandonment in the Loess Plateau, China. Land Degradation & Development, 30(14): 1677–1690.

Liu M Y, Li P, Liu M M, et al. 2021. The trend of soil organic carbon fractions related to the successions of different vegetation types on the tableland of the Loess Plateau of China. Journal of Soils and Sediments, 21(1): 203–214.

Liu W X, Xu W H, Hong J P, et al. 2010. Interannual variability of soil microbial biomass and respiration in responses to topography, annual burning and N addition in a semiarid temperate steppe. Geoderma, 158(3–4): 259–267.

Liu Y F, Meng L C, Huang Z, et al. 2022. Contribution of fine roots mechanical property of Poaceae grasses to soil erosion resistance on the Loess Plateau. Geoderma, 426: 116122, doi: 10.1016/j.geoderma.2022.116122.

Liu Y L, Song X Z, Wang K B, et al. 2022. Changes in soil microbial metabolic activity following long-term forest succession on the central Loess Plateau, China. Land Degradation & Development, 34(3): 723–735.

Liu Z Y, Michalet R, Wang C Y, et al. 2023. Contrasting effects of two phenotypes of an alpine cushion plant on understory species drive community assembly. Science of the Total Environment, 859: 160154, doi: 10.1016/j.scitotenv.2022.160154.

Lozano Y M, Hortal S, Armas C, et al. 2014. Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. Soil Biology and Biochemistry, 78: 298–306.

Lucas-Borja M E, Hedo J, Cerda A, et al. 2016. Unravelling the importance of forest age stand and forest structure driving microbiological soil properties, enzymatic activities and soil nutrients content in Mediterranean Spanish black pine (*Pinus nigra* Ar. ssp *salzmannii*) Forest. Science of the Total Environment, 562: 145–154.

Lucas-Borja M E, Delgado-Baquerizo M. 2019. Plant diversity and soil stoichiometry regulates the changes in multifunctionality during pine temperate forest secondary succession. Science of the Total Environment, 697: 134204, doi: 10.1016/j.scitotenv.2019.134204.

Luo Y, Xiao H B, Wu X, et al. 2022. Mitigation of nutrient runoff loss using reduced nitrogen application and green manure planting in citrus orchard in Hubei, China. Journal of Soils and Sediments, 23(2): 582–595.

Marriott C A, Hudson G, Hamilton D, et al. 1997. Spatial variability of soil total C and N and their stable isotopes in an upland Scottish grassland. Plant and Soil, 196(1): 151–162.

O'dea J K, Jones C A, Zabinski C A, et al. 2015. Legume, cropping intensity, and N-fertilization effects on soil attributes and processes from an eight-year-old semiarid wheat system. Nutrient Cycling in Agroecosystems, 102(2): 179–194.

O'Halloran L R, Borer E T, Seabloom E W, et al. 2013. Regional contingencies in the relationship between aboveground biomass and litter in the world's grasslands. PloS ONE, 8(2): e054988, doi: 10.1371/journal.pone.0054988.

Ohtsuka T, Shizu Y, Nishiwaki A, et al. 2010. Carbon cycling and net ecosystem production at an early stage of secondary succession in an abandoned coppice forest. Journal of Plant Research, 123(4): 393–401.

Olsen S R, Sommers L E, Page A L. 1982. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties of Phosphorus. Madison: American Society of Agronomy, 403–430.

Peichl M, Leava N A, Kiely G. 2012. Above- and belowground ecosystem biomass, carbon and nitrogen allocation in recently afforested grassland and adjacent intensively managed grassland. Plant and Soil, 350(1–2): 281–296.

Plaza C, Hernandez D, Garcia-Gil J C, et al. 2004. Microbial activity in pig slurry-amended soils under semi-arid conditions. Soil Biology and Biochemistry, 36(10): 1577–1585.

Qiu D X, Xu R R, Wu C X, et al. 2022. Vegetation restoration improves soil hydrological properties by regulating soil physicochemical properties in the Loess Plateau, China. Journal of Hydrology, 609: 127730, doi: 10.1016/j.jhydrol.2022.127730.

Reich P B. 2005. Global biogeography of plant chemistry: Filling in the blanks. New Phytologist, 168(2): 263–266.

Ren C J, Kang D, Wu J P, et al. 2016a. Temporal variation in soil enzyme activities after afforestation in the Loess Plateau, China. Geoderma, 282: 103–111.

Ren C J, Zhao F, Kang D, et al. 2016b. Linkages of C:N:P stoichiometry and bacterial community in soil following afforestation of former farmland. Forest Ecology and Management, 376: 59–66.

Ren C J, Chen J, Deng J, et al. 2017. Response of microbial diversity to C:N:P stoichiometry in fine root and microbial biomass following afforestation. Biology and Fertility of Soils, 53(4): 457–468.

Ren C J, Wang T, Xu Y D, et al. 2018. Differential soil microbial community responses to the linkage of soil organic carbon fractions with respiration across land-use changes. Forest Ecology and Management, 409: 170–178.

Sidlauskaite G, Kemesyte V, Toleikiene M, et al. 2022. Plant diversity, functional group composition and legumes effects versus fertilisation on the yield and forage quality. Sustainability, 14(3): 1182, doi: 10.3390/su14031182.

Sivaram A K, Logeshwaran P, Subashchandrabose S R, et al. 2018. Comparison of plants with C_3 and C_4 carbon fixation pathways for remediation of polycyclic aromatic hydrocarbon contaminated soils. Scientific Reports, 8: 2100, doi: 10.1038/s41598-018-20317-0.

Song G, Hui R, Yang H T, et al. 2022. Biocrusts mediate the plant community composition of dryland restoration ecosystems. Science of the Total Environment, 844: 157315, doi: 10.1016/j.scitotenv.2022.157135.

Sun C, Chai Z, Liu G, et al. 2017. Changes in species diversity patterns and spatial heterogeneity during the secondary succession of grassland vegetation on the Loess Plateau, China. Frontiers in Plant Science, 8: 1465, doi: 10.3389/fpls.2017.01465.

Sun Y, Chen L, Zhang S Y, et al. 2022. Plant interaction patterns shape the soil microbial community and nutrient cycling in different intercropping scenarios of aromatic plant species. Frontiers in Microbiology, 13: 888789, doi: 10.3389/fmicb.2022.888789.

Ter Braak C J, Smilauer P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). [2022-10-12]. http://www.canoco.com.2012-496.

Tessema Z K, Belay E F. 2017. Effect of tree species on understory vegetation, herbaceous biomass and soil nutrients in a semi-arid savanna of Ethiopia. Journal of Arid Environments, 139: 76–84.

Tian F P, Zhang Z N, Chang X F, et al. 2016. Effects of biotic and abiotic factors on soil organic carbon in semi-arid grassland. Journal of Soil Science and Plant Nutrition, 16(4): 1087–1096.

van der Heijden M G A, Bardgett R D, van Straalen N M. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters, 11(3): 296–310.

van der Putten W H, Bardgett R D, Bever J D, et al. 2013. Plant-soil feedbacks: The past, the present and future challenges. Journal of Ecology, 101(2): 265–276.

Walker L R, Wardle D A, Bardgett R D, et al. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology, 98(4): 725–736.

Wang G L, Liu G B, Xu M X. 2009. Above- and belowground dynamics of plant community succession following abandonment of farmland on the Loess Plateau, China. Plant and Soil, 316(1–2): 227–239.

Wang L L, Zhang G H, Zhu P Z, et al. 2022. Soil C, N and P contents and their stoichiometry as affected by typical plant communities on steep gully slopes of the Loess Plateau, China. CATENA, 208: 105740, doi: 10.1016/j.catena.2021.105740.

Wardle D A, Ghani A. 1995. A critique of the microbial metabolic quotient (qCO_2) as a bio-indicator of disturbance and ecosystem development. Soil Biology & Biochemistry, 27(12): 1601–1610.

Wickander N J, Rasmussen P U, Marteinsdottir B, et al. 2021. Ecological and evolutionary responses of an arctic plant to variation in microclimate and soil. Oikos, 130(2): 211–218.

Williams M A, Jangid K, Shanmugam S G, et al. 2013. Bacterial communities in soil mimic patterns of vegetative succession and ecosystem climax but are resilient to change between seasons. Soil Biology and Biochemistry, 57: 749–757.

Wu G L, Liu Y, Tian F P, et al. 2017. Legumes functional group promotes soil organic carbon and nitrogen storage by increasing plant diversity. Land Degradation & Development, 28(4): 1336–1344.

Xiao C W, Zhou Y, Su J Q, et al. 2017. Effects of plant functional group loss on soil microbial community and litter decomposition in a steppe vegetation. Frontiers in Plant Science, 8: 2040, doi: 10.3389/fpls.2017.02040.

Xiao J, Wang B L, Qiu X L, et al. 2021. Interaction between carbon cycling and phytoplankton community succession in hydropower reservoirs: Evidence from stable carbon isotope analysis. Science of the Total Environment, 774: 145141, doi: 10.1016/j.scitotenv.2021.145141.

Yahdjian L, Tognetti P M, Chaneton E J. 2017. Plant functional composition affects soil processes in novel successional grasslands. Functional Ecology, 31(9): 1813–1823.

Yang T, Song L Y, Lin H Y, et al. 2023. Within-species plant phylogeny drives ectomycorrhizal fungal community composition in tree roots along a timberline. Soil Biology and Biochemistry, 176: 108880, doi: 10.1016/j.soilbio.2022.108880.

Yang Y, Liang C, Wang Y Q, et al. 2020. Soil extracellular enzyme stoichiometry reflects the shift from P- to N-limitation of microorganisms with grassland restoration. Soil Biology and Biochemistry, 149: 107928, doi: 10.1016/j.soilbio.2020.107928.

Yao Z Y, Xu Q, Chen Y P, et al. 2021. Leguminous green manure enhances the soil organic nitrogen pool of cropland via disproportionate increase of nitrogen in particulate organic matter fractions. CATENA, 207: 105574, doi: 10.1016/j.catena.2021.105574.

Zeng Q, An S, Liu Y. 2017. Soil bacterial community response to vegetation succession after fencing in the grassland of China. Science of the Total Environment, 609: 2–10.

Zhang C, Liu G B, Xue S, et al. 2011. Rhizosphere soil microbial activity under different vegetation types on the Loess Plateau, China. Geoderma, 161(3–4): 115–125.

Zhang C, Liu G B, Xue S, et al. 2016. Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. Soil Biology and Biochemistry, 97: 40–49.

Zhang D B, Zhang C, Ren H L, et al. 2021. Trade-offs between winter wheat production and soil water consumption via leguminous green manures in the Loess Plateau of China. Field Crops Research, 272: 108278, doi: 10.1016/j.fcr.2021.108278.

Zhang J T. 2005. Succession analysis of plant communities in abandoned croplands in the eastern Loess Plateau of China. Journal of Arid Environments, 63(2): 458–474.

Zhang W, Gao D, Chen Z, et al. 2018a. Substrate quality and soil environmental conditions predict litter decomposition and drive soil nutrient dynamics following afforestation on the Loess Plateau of China. Geoderma, 325: 152–161.

Zhang W, Qiao W, Gao D, et al. 2018b. Relationship between soil nutrient properties and biological activities along a restoration chronosequence of *Pinus tabulaeformis* plantation forests in the Ziwuling Mountains, China. CATENA, 161(Suppl. C): 85–95.

Zhang X Y, Zhao W Q, Liu Y J, et al. 2022. Dominant plant species and soil properties drive differential responses of fungal communities and functions in the soils and roots during secondary forest succession in the subalpine region. Rhizosphere, 21: 100483, doi: 10.1016/j.rhisph.2022.100483.

Zhang Y H, Xu X L, Li Z W, et al. 2021. Improvements in soil quality with vegetation succession in subtropical China Karst. Science of the Total Environment, 775: 145876, doi: 10.1016/j.scitotenv.2021.145876.

Zhao F Z, Kang D, Han X, et al. 2015. Soil stoichiometry and carbon storage in long-term afforestation soil affected by understory vegetation diversity. Ecological Engineering, 74: 415–422.

Zhao F Z, Ren C J, Han X H, et al. 2018. Changes of soil microbial and enzyme activities are linked to soil C, N and P stoichiometry in afforested ecosystems. Forest Ecology and Management, 427: 289–295.

Zhao F Z, Bai L, Wang J Y, et al. 2019. Change in soil bacterial community during secondary succession depend on plant and soil characteristics. CATENA, 173: 246–252.

Zheng F L. 2006. Effect of vegetation changes on soil erosion on the Loess Plateau. Pedosphere, 16(4): 420–427.

Zheng Y, Hu Z K, Pan X, et al. 2021. Carbon and nitrogen transfer from litter to soil is higher in slow than rapid decomposing plant litter: A synthesis of stable isotope studies. Soil Biology and Biochemistry, 156: 108196, doi:

10.1016/j.soilbio.2021.108196.

Zhou Z H, Wang C K, Jiang L F, et al. 2017. Trends in soil microbial communities during secondary succession. Soil Biology and Biochemistry, 115: 92–99.

Zhu H H, He X Y, Wang K L, et al. 2012. Interactions of vegetation succession, soil bio-chemical properties and microbial communities in a Karst ecosystem. European Journal of Soil Biology, 51: 1–7.

Zhu P Z, Zhang G H, Wang C S, et al. 2021a. Variation in land surface roughness under typical plant communities on steep gully slopes on the Loess Plateau of China. CATENA, 206: 105549, doi: 10.1016/j.catena.2021.105549.

Zhu P Z, Zhang G H, Wang H X, et al. 2021b. Effectiveness of typical plant communities in controlling runoff and soil erosion on steep gully slopes on the Loess Plateau of China. Journal of Hydrology, 602: 126714, doi: 10.1016/j.jhydrol.2021.126714.

Zou H, Gao G Y, Yuan C, et al. 2022. Interactions between soil water and plant community during vegetation succession in the restored grasslands on the Loess Plateau of China. Land Degradation & Development, 34(5): 1582–1592.

Appendix

Table S1 Geographical features and dominant species at different plots

Plot	Slope degree (°)	Aspect (°)	Elevation (m)	Location	Dominant species
Farmland	26	North by east 45	1187.3	36°46′N, 109°15′E	-
5 a	28	North by west 40	1152.4	36°45′N, 109°15′E	*A. capillaris*, *H. altaicus*
10 a	30	North by east 55	1239.1	36°44′N, 109°16′E	*S. bungeana*, *A. capillaris*
18 a	27	North by west 38	1195.6	36°45′N, 109°16′E	*L. dahurica*, *A. sacrorum*
30 a	32	North by east 42	1251.2	36°44′N, 109°16′E	*A. giraldii*, *L. dahurica*, *B. ischaemum*

Note: *A. capillaris*, *Artemisia capillaris* Thunb.; *H. altaicus*, *Heteropappus altaicus* (Willd.) Novopokr; *S. bungeana*, *Stipa bungeana* Trin.; *L. dahurica*, *Lespedeza dahurica* Schindler; *A. sacrorum*, *Artemisia sacrorum* Ledeb.; *A. giraldii*, *Artemisia giraldii* Pamp.; *B. ischaemum*, *Bothriochloa ischaemum* (Linnaeus) Keng. - indicates no dominant species.

Table S2 Methods for determination of soil enzymatic activities

Type of enzyme	Detailed measurement method
Soil catalase activity	Soil catalase activity was determined by addition of 40 mL distilled water and 5 mL 0.3% H_2O_2 to 2 g fresh soil. The mixture was shaken for 20 min (at 150 r/m) and filtered (Whatman 2V) immediately. Then the filtrate was titrated with 0.1 mol/L $KMnO_4$ under the conditions of sulfuric acid. Finally, the results were expressed as 0.1 mol $KMnO_4$/(g•20 min).
Soil saccharase activity	Soil saccharase activity was determined using 8% glucose solution as substrates. About 5 g fresh soil was incubated with 15 mL substrates, 5 mL 0.2 M phosphate buffer (pH 5.5), and 5 drops of toluene for 24 h at 37.8°C. After incubation, the mixture was filtered (Whatman 2V) immediately and 1-mL aliquot was reacted with 3 mL 3, 5-dinitrylsalicylate in a volumetric flask, and then heated for 5 min. Soil solution in the flask was quantified in an ultraviolet spectrometer subsystem (UVS) at 508 nm when it reached room temperature. Finally, results were also expressed as mg glucose/(g•24 h).
Soil urease activity	Soil urease activities was routinely determined using 10% urea solution as substrates. About 5 g fresh soil was incubated for 24 h at 37.8°C with 5 mL citrate solution at pH 6.7 and 5 mL substrates. The reaction mixture was then diluted to 50 mL with distilled water. After incubation, the mixture was immediately filtered and 1 mL supernatant was treated with 4 mL sodium phenol solution and 3 mL 0.9% sodium hypochlorite solution. The released ammonium released from urea hydrolysis was quantified in an ultraviolet spectrometer subsystem (UVS) at 578 nm. Results were expressed as mg NH_4^+-N/(g•24 h).
Soil alkaline phosphatase activity	Soil alkaline phosphatase activity was determined by addition of 10 g fresh soil, 2 mL toluene, 10 mL disodium phenyl phosphate solution, and 10 mL 0.05 M borate buffer. The reaction mixture was incubated for 2 h at 37.8°C. After incubation, the mixture was immediately filtered, then the filtrate was treated with 0.5 mL of 2% 4-aminoantipyrine and 8% potassium ferrocyanide; the phenol released was determined in an ultraviolet spectrometer subsystem (UVS) at 510 nm. Results were expressed as mg phenol/(g•24 h).

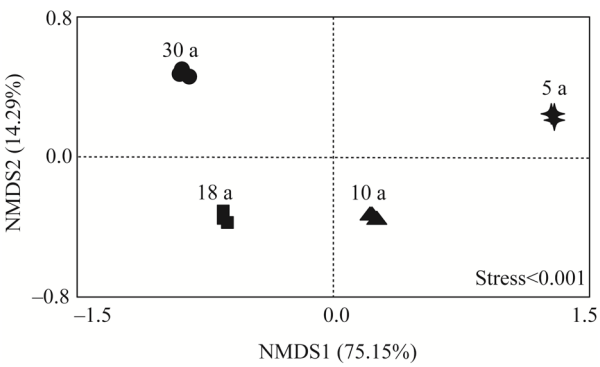

Fig. S1 Nonmetric multidimensional scaling (NMDS) analysis of plant community composition over successional time

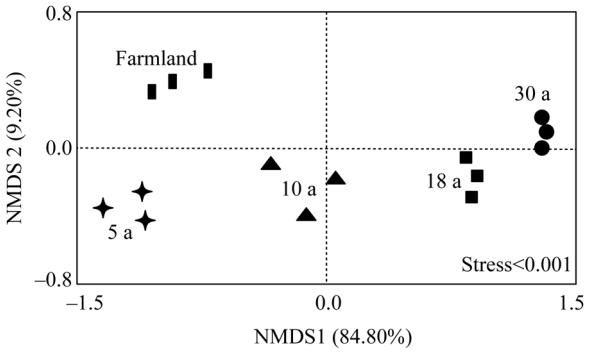

Fig. S2 Nonmetric multidimensional scaling (NMDS) analysis of soil physical-chemical properties over successional time

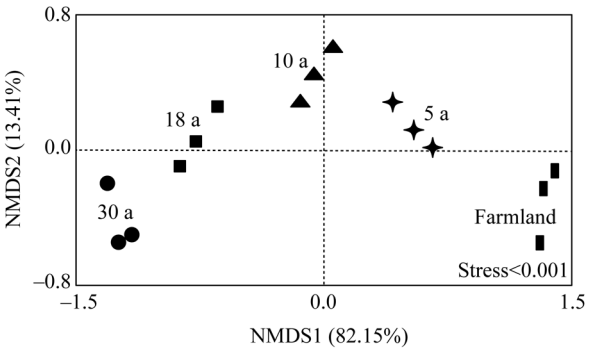

Fig. S3 Nonmetric multidimensional scaling (NMDS) analysis of soil biological properties over successional time